

UTAH FLORA: CACTACEAE

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ABSTRACT.—The Cactaceae of Utah are revised. Keys to genera, species, and infraspecific taxa are provided. The taxa are provided with descriptions and geographical and other pertinent data. New nomenclatural combinations include *Sclerocactus pubispinus* (Engelm.) L. Benson var. *spinosior* (Engelm.) Welsh and *Sclerocactus whipplei* (Engelm.) Britt. & Rose var. *glaucus* (K. Schum.) Welsh.

Classification of cacti has been regarded as difficult, and our Utah taxa are not exceptions. Many factors combine to cause this difficulty. Morphologically similar flowers, at least in some of the genera, have forced workers to use vegetative characteristics such as stem and spine structure, nature of the areoles, presence or absence of surface coverings, shape and number of ribs or tubercles, and nature of hypogeous features for purposes of differentiation. Flowers, even within a taxon, may show great color amplitude. Additionally, workers have relied on the nature of the fruit, and, even in those years when fruits are formed, they are present for only a small portion of the year. The use of fruits by insects as incubation chambers for larvae makes this organ, in otherwise dry-fruited taxa, resemble fleshy fruits. Also, such infested fruits often are the only ones seen, as they persist after healthy fruits have matured and fallen.

Longtime workers in this field have typically used a common garden approach to avoid phenotypic variation as representing genotypic differences. But that approach has also led to problems because phenotypes in common garden grown plants sometimes lack similarity with the plants grown under field conditions, and attempts to identify field-grown plants by use of keys to identification based on the garden-grown ones often fail.

Paucity or lack of diagnostic reproductive morphology imposes a different kind of attempt at classification, wherein taxonomic groups are sometimes (perhaps often) based on analogies, not on homologies. Thus, the systems of classification of cacti tend to be

artificial, with the taxonomic units sometimes representing convenience rather than relationship. The plants with vegetative parts appearing alike can have separate possible origins, and because they look alike they are placed together—though they might be but distantly related or completely unrelated. Possibly because of the artificial nature of the taxa, there are more infraspecific taxa than would seem warranted in other families of similar size; in Utah we have 28 species and 20 varieties, or a total of 48 taxa. Eleven of the species, or about 40 %, have two or more varieties.

Problems likewise involve breeding systems in the cacti. Hybridization is rampant in some genera, especially so in *Opuntia*, subgenus *Opuntia*, where almost every conceivable combination of hybridity is available in the field and is represented by specimens in the herbarium. Genetic barriers to hybridization seem to be lacking or essentially so. The plants, once established, have a great potential longevity. The presence of heterozygosity does not seem to affect that longevity, and it may increase the possibility of survival in more diverse habitats.

Problems of understanding cactus taxonomy have not been aided by the attraction of cacti to a large group of more or less well-trained admirers, some of whom have attempted, with varied success, to resolve nomenclatural and taxonomic difficulties. Some workers have studied the group from afar, and each variant has seemed worthy of being named. The named entities are then sought by other cactus fans, in an extension of the trophy syndrome. Professional workers in the

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family have sometimes attempted to diminish collecting by trophy hunters and commercial gatherers by withholding information on collection localities, making further legitimate work difficult if not impossible. Into this tangled jungle of nomenclatural and taxonomic problems struggled Lyman Benson, whose life work on the cacti (1982) represents the first overview of the family for North America north of Mexico and the most realistic approach to undoing the Gordian knot created by all those who had worked with the group prior to him. Because of his tremendous contribution to an understanding of the Cactaceae, this meager work is dedicated to him.

Tolerance to varied ecological conditions evidently results in different phenotypical responses, even when the genotype is more or less homogenous. Thus, plants from shaded slopes may have a different appearance than those in the more open area nearby.

Ecologically many of the cactus species are opportunists, taking advantage of reduction of more palatable range vegetation, thereby increasing under heavy utilization by livestock in some areas. Cacti are thought of as indicators of drought situations, but some species show great ecological amplitude, occurring from dry low elevation areas upward to mesic high elevation sites. The greater bulk of them occur in the southernmost counties, especially in Washington County with its extension of the Mojave Desert vegetative type. Cacti are present in every county in Utah, however.

Cacti are generally armed with spines, which are straight, curved, or twisted; erect, spreading, or deflexed; smooth or barbed; variously colored; flattened or terete; or in some species and forms lacking altogether. The spines serve to protect the plants from predation and grazing by inflicting mechanical injury to animals and humans. Some birds, however, have learned to take advantage of certain of the cacti by building nests among the protective curtain of spines, i.e., the cactus wren. The *Opuntias* have other features that protect them. In subgenus *Cylindropuntia* the epidermis of the spines is deciduous, forming a sheath that remains within the puncture wound when animals contact the sharp spines. Additionally, all *Opuntias*

produce neatly packed multirowed, retrorsely barbed spinules known as glochids. The glochids are borne in the upper portion of the areoles, specialized areas at the nodes (often on tubercles). This upper portion of the areole is also the area capable of continued growth, and new glochids seem to form each year on some *Opuntia*. The glochids are easily detachable by even gentle contact with animal skin. The sharp points penetrate the skin and are locked in place by the retrorse barbs, forming a subvisible burning irritant that reminds one of its presence with each contact with some surface, even following diminution of the initial burning sensation.

Because of their form, armament, and ability to hold water, usually as bound water in complex colloidal systems, botanists have been reluctant to make collections. The present study is based on the examination of 606 specimens, and the writer has collected only 173 of those. The preservation of an adequate herbarium specimen requires time, patience, and suffering. Because of these problems, and because the specimens thus produced are often offensive to the aesthetic senses of botanists, they are collected only by persons of great devotion or dullness. Hence, botanical collection seldom provides much voucher material for definitive taxonomic judgments, and little possibility exists of depletion of natural populations by botanical collectors. The cacti are a miserable group with which to work and, except as botanical curiosities, they would have received little attention.

Fortunately, commercial gathering of cactus species in Utah has not been extensive. Our marketable cacti are few, and with one or two exceptions there seems to be little future in gathering cacti commercially in Utah.

The flowers of cacti are, however, among the most beautiful of all plants in Utah. The numerous petals (petaloids) vary from white to yellowish, greenish, yellow, golden, bronze, pink, violet, pink-purple, violet-purple, red, and scarlet, each taking on an almost fluorescent hue due to shape of individual cells in their surfaces. Photographs seldom do justice to the beauty of the plants; they are best viewed in their natural habitats, where the mind serves to judge the intense beauty and to hold that vivid impression in memory.

CACTACEAE

Cactus Family

Perennial succulent woody or herbaceous plants, with spiny, glochidiate, or rarely unarmed, globose, cylindric, columnar, or flattened stems; stems ribbed, smooth, or tuberculate; leaves lacking, or green, terete, and caducous (*Opuntia*); areoles axillary (regardless of apparent position), bearing wool,

glochids, spines, branches, or flowers; perianth of numerous segments grading from sepals to petals, imbricate, the bases more or less united, inserted on a hypanthium; stamens numerous, variously inserted within the hypanthium tube; style 1; stigmatic lobes several; ovary inferior; fruit a dry or fleshy many-seeded berry.

BENSON, L. 1982. The cacti of the United States and Canada. Stanford Univ. Press, California. 1044 pp.

1. Stems jointed, the joints flattened, clavate, or cylindric; areoles with glochids and spines (or spineless), subtended by caducous terete green leaves when young *Opuntia*
- Stems hemispheric or cylindroid, not jointed; areoles with hair or spines but no glochids 2
- 2(1). Flowers borne in axils of tubercles or at bases of grooves, removed from the spiniferous areoles; central spine hooked, dark purple; small hemispheric or cylindrical plants of Washington County *Mammillaria*
- Flowers borne variously, seldom as above; central spines hooked or straight, but if hooked then not of Washington County 3
- 3(2). Stems with tubercles spirally arranged; tubercles distinctly grooved on upper side; flowers pink or yellow *Coryphantha*
- Stems ribbed; tubercles not grooved; flowers variously colored 4
- 4(3). Flowers borne laterally below the stem apex; hypanthium spiny *Echinocereus*
- Flowers terminal on the stems; hypanthium devoid of spines 5
- 5(4). Stems 20–50 cm in diameter or more, mainly 2–10 dm tall; upper axils and ovaries not woolly; plants of Washington County *Ferocactus*
- Stems usually much smaller, or if, as rarely, approaching the lower limits as described above, the ovaries and upper axils woolly 6
- 6(5). Stems mainly 12–25 cm in diameter; spines flattened, annular; ovaries and upper axils woolly; plants rare in Kane (?) and Washington counties *Echinocactus*
- Stems mainly 3–10 cm in diameter; spines variously terete, subterete, or flattened, but not annular; ovaries and upper axils not or rarely woolly 7
- 7(6). Spines straight, purplish or reddish, 2–5 cm long or more; flowers rose-pink; plants of the Beaver Dam Mountains, Washington County *Neolloydia*
- Spines hooked or some or all of them straight; flowers variously colored; plants not of western Washington County, or if so then the flowers yellow 8
- 8(7). Stems with spines all straight, depressed-hemispheric; flowers white to yellow or pale pinkish, mainly 1–2 cm long *Pediocactus*
- Stems with at least some spines hooked, or if straight, then flowers rose-pink to violet or more than 2 cm long *Sclerocactus*

CORYPHANTHA (Engelm.) Lem.

Plants depressed-hemispheric to hemispheric or shortly cylindric, solitary or colonial; tubercles separate; areoles circular;

spines smooth; central spines 0 or 3–12 per areole, transitional to radials, straight, elliptic in cross-section; radial spines 12–40 per areole, straight, subterete; flowers axillary at

tubercle base, at end of a felty persistent groove connected to the areole, borne near the summit of the stem; flowers funnelform,

the perianth pink-purple to rose or yellow; fruit fleshy, green or red, indehiscent; seeds black or brown.

- 1. Flowers yellow; fruit red at maturity, globular; plants rare in Garfield and Kane counties *C. missouriensis*
- Flowers pink-purple to rose; fruit green at maturity, ellipsoid; plants widely distributed *C. vivipara*

***Coryphantha missouriensis* (Sweet) Britt. & Rose** [*Mammillaria missouriensis* Sweet]. Stems commonly solitary, depressed hemispheric, 2–5 cm tall, 3–8 cm wide; tubercles 6–9 mm long; areoles few; radial spines 10–19, spreading; flowers 3.8–5 cm wide and long; sepaloids greenish, the margins yellowish or whitish; petaloids yellow; filaments yellow; anthers yellow; style green, 12–25 mm long; fruit red, ca 1 cm thick; seeds black, 2–2.5 mm wide. Cool desert shrub, juniper, and ponderosa pine communities in Garfield (type of variety from Hells Backbone) and Kane (lectotype of variety from Buckskin Mts.) counties; Arizona. Our material belongs to **var. *marstonii* (Clover) Benson** [*C. marstonii* Clover]; 1 (0). The species is distributed from Montana east to North

Dakota, south to Arizona, New Mexico, and Texas.

***Coryphantha vivipara* (Nutt.) Britt. & Rose** [*Cactus viviparus* Nutt.]. Stems solitary or colonial, depressed hemispheric to short-cylindric, mainly 2–15 cm tall, 2–10 cm wide; tubercles 6–9 mm long; areoles 1.5–3 mm wide; central spines 3–12, whitish basally, dark apically, mainly 12–20 mm long; radial spines 12–20, spreading, obscuring the stem; flowers 2.5–5 cm wide and long; sepaloids greenish, the margins variously colored; petaloids pink-purple or rose; anthers yellow; fruit green, ellipsoid, 12–25 mm long; seeds brown, reticulate, 1.5–2 mm wide. Three more or less distinctive varieties are present in Utah.

- 1. Central spines 4; flowers ca 3.8 cm wide; plants of Carbon and Uintah counties *C. vivipara* var. *vivipara*
- Central spines 4–7; flowers wider or if narrower then not of northeastern Utah 2
- 2(1). Flowers about 2.5–3 cm wide; radial spines 12–20, 9–12 mm long; petaloids yellowish, greenish, or pinkish; plants of Washington County .. *C. vivipara* var. *deserti*
- Flowers mainly 3.8–5 cm wide; radial spines 20–30; petaloids pink-purple to rose; plants rather broadly distributed *C. vivipara* var. *arizonica*

Var. *arizonica* (Engelm.) W. T. Marshall [*Mammillaria arizonica* Engelm.]. Desert shrub and pinyon-juniper communities at 1586 to 2440 m in Beaver, Garfield, Juab, Kane, Millard, Piute, San Juan, Sevier, Tooele, Washington, and Wayne counties; Nevada to Colorado, south to Arizona and New Mexico; 23 (xiii). This variety is locally common on limestone and dolomite outcrops and on gravels degraded from them. It is a beautiful plant when in flower, the violet flowers contrasting with the thatch of whitish spines. Like other of our depressed-hemispheric cacti, the plants expand as they take up water in springtime. Following flowering, the plants dry and shrink downward into the

substrate surface. Plants conspicuous at flowering become difficult to observe when dormant. The juice of *Coryphantha vivipara* is apparently unique among our species in being non-mucilaginous.

Var. *deserti* (Engelm.) W. T. Marshall [*Mammillaria deserti* Engelm.; *M. chlorantha* Engelm., type from St. George]. The small yellowish to pinkish flowers are apparently diagnostic. Warm desert shrub communities at 760 to 980 m in Washington County; Arizona, Nevada, and California; 2 (i).

Var. *vivipara*. Desert shrub and pinyon juniper communities in Carbon and Duchesne counties; Alberta to Manitoba, south to Oregon, New Mexico, and Texas; 1 (0).

ECHINOCACTUS Link & Otto

Stems solitary or few to many, subglobose to cylindric, woolly at the apex, few- to many-ribbed; areoles large; spines broad, flattened-triangular, with transverse annular rings; flowers borne subapically, yellow; floral tube bearing spiny persistent scales; ovary clothed with narrow scales having mats of wool; fruit densely white-woolly, dry at maturity; seeds black, shining.

- 1. Spines felty, at least when young; seeds papillate, dull or shining from the papillae; plants of Washington County *E. polycephalus* var. *polycephalus*
- Spines smooth or with scattered hairs; seeds smooth and shining; plants of Kane (?) County *E. polycephalus* var. *xeranthemoides*

Var. *polycephalus*. Warm desert shrubland on the Beaver Dam slope, Washington County (reported by Meyer); Nevada, California, and Arizona; 0 (0).

Var. *xeranthemoides* Coulter. Pinyon-juniper and desert shrub communities near Kanab, Kane County, Arizona; a Plateau endemic; 0 (0). This report is based on two collections by pioneer collectors, one by A. L. Siler (in "Kanab Mts.") in 1881 and the other by Dr. E. Palmer in 1877 (in "S. Utah"). Since it is probable that neither knew where the Utah-Arizona boundary was situated (it was surveyed in 1879), the collections noted could have been taken from nearby

Echinocactus polycephalus Engelm. & Bigel. Stems mostly 2-3 dm tall and 1-2 dm thick (or more); ribs 10-21; areoles 10-12 mm long; radial spines 8-10, 2.5-5 cm long, often reddish when young, subulate, triangular-flattened; central spines 3-5, stouter than the radial, annulate, curved but not hooked, 3-8 cm long; flowers 5-6 mm long, yellow; perianth segments narrowly oblong; fruits 15-25 mm long, dehiscent by a basal pore; seeds angular, black. Two varieties are potentially present in Utah.

Arizona. However, the plants should be sought near Kanab.

ECHINOCEREUS Engelm. in Wisliz.

Stems erect or ascending, solitary or more usually colonial, cylindric or subcylindric; areole small; central spines 1-6; radial spines 5-12, acicular to subulate, flattened or subterete; flowers borne laterally, below the stem apex, the bud breaking through the epidermis above the areole, large and showy, pink-purple to scarlet; stigmas green; fruit fleshy, spiny, not regularly dehiscent, the spine clusters deciduous as fruit matures.

- 1. Flowers pink-purple to rose; stems solitary or few, often over 10 cm tall *E. engelmannii*
- Flowers scarlet; stems often 10 cm long or less, few to numerous in compact hemispheric clusters *E. triglochidiatus*

***Echinocereus engelmannii* (Parry) Lem.** [*Cereus engelmannii* Parry]. Stems solitary or 2 to several (or rarely many) and loosely clustered, mainly 10-30 cm tall, 5-9 cm thick; ribs 10-13; tubercles not prominent; areoles small, subcircular; central spines 2-6, stout, more or less curved or twisted, 2-5 cm long; radial spines 6-12, 7-15 mm long, appressed and spreading; flowers 5-9 cm long, pink-purple to rose; perianth segments oblong; fruit ovoid to oblong, green or turning red,

the spine clusters deciduous; seeds black, globose, pitted, 1-1.5 mm long. This widely ranging southwestern species consists of a series of morphologically differing but intergrading segregates, which largely lack geographical integrity. Utah material has been assigned to three of the named segregates (Benson 1982). The following tentative key will serve to allow application of names to most specimens.

- 1. General aspect of spines purplish-black, with some grayish ones apically or intermixed; stems mainly 15-30 cm tall; plants of warm desert shrub communities in south central Washington County *E. engelmannii* var. *purpureus*

- General aspect of spines grayish, with some purplish black ones apically or intermixed; stems often 10–20 cm tall; plants of various distribution 2
- 2(1). Lowermost central spines mainly 3.5–6 cm long, not markedly differing in color from the other spines; plants of canyons of the Colorado
..... *E. engelmannii* var. *variegatus*
- Lowermost central spines mainly 2.8–4.5 cm long, often markedly differing in color from other spines; plants mainly not of the Colorado canyons
..... *E. engelmannii* var. *chrysocentrus*

Var. *chrysocentrus* (Engelm. & Bigel.) Engelm. ex Rumpler [*Cereus engelmannii* var. *chrysocentrus* Engelm. & Bigel.]. Larrea, Joshua tree, shadscale, and mountain brush communities at 760 to 1865 m in Beaver, Juab, Kane (inter var. *variegatus*), Millard, and Washington counties; Nevada, California, and Arizona; 18 (v).

Var. *purpureus* L. Benson Blackbrush community at 915 to 1130 m in south central Washington Co. (type from 1 mi N St. George); endemic; 16 (i). This dark-spined phase of hedgehog cactus is transitional to var. *chrysocentrus*. Interpreted broadly, it includes specimens from near Leeds to west of Santa Clara, and might be regarded as a dark-spined phase of var. *chrysocentrus*. But the degree of integrity is about the same as for infraspecific taxa elsewhere in the Cactaceae, and it seems best to recognize this entity at some taxonomic rank.

Var. *variegatus* (Engelm. & Bigel.) Engelm. ex Rumpler [*Cereus engelmannii* var. *variegatus* Engelm. & Bigel.]. Black-

brush, shadscale, and pinyon-juniper communities at 1125 to 1895 m in Garfield, Kane, and San Juan counties; Arizona; 6 (ii). Purported differences between this phase of the species complex and those noted for var. *chrysocentrus* are tenuous, and the two phases could be combined without doing serious injustice to their taxonomy.

***Echinocereus triglochidiatus* Engelm.** [*E. coccineus* Engelm.]. Stems few to several hundred in compact hemispheric clumps or mounds, mainly 8–15 cm long, 3–6 cm thick; ribs 9 or 10, the tubercles not prominent; areoles circular, bearing a white felty mat when young; central spines 1–3, 8–40 mm long or more, stout, straight or curved to twisted; radial spines 5–8, 4–35 mm long, not appressed, spreading; flowers 5–7.5 mm long, scarlet; perianth segments cuneate-obovate; fruit red at maturity, obovoid to cylindroid; seeds papillate, 1.5–2 mm long. Three rather weakly separable varieties are present in Utah.

- 1. Areoles spineless or with spines less than 3 mm long; plants of San Juan and adjacent Grand counties *E. triglochidiatus* var. *inermis*
- Areoles armed, the spines mainly 4–40 mm long or more; plants of broad but different distribution 2
- 2(1). Central spines twisting or curved; flowers often over 4 cm wide; plants of Millard, Beaver, and Washington counties *E. triglochidiatus* var. *mojavensis*
- Central spines straight; flowers often less than 4 cm wide; plants of broad distribution *E. triglochidiatus* var. *melanacanthus*

Var. *inermis* (K. Schum.) Rowley [*E. phoeniceus* var. *inermis* K. Schum.]. Salt desert shrub-pinyon-juniper vegetative types at ca 1525 m in San Juan and Grand (?) counties; Colorado; a Plateau endemic; 1 (i). The type was taken from the La Sal Mts. Benson (1982) treats this plant in synonymy under var. *melanacanthus*, but it has about the

same degree of morphological and geographic integrity as do other phases regarded as varieties. It is recognized herein mainly to draw attention to its existence.

Var. *melanacanthus* (Engelm.) L. Benson [*Cereus coccineus* var. *melanacanthus* Engelm.]. Blackbrush, Ephedra, sagebrush, pinyon-juniper, mountain brush, and aspen

communities at 975 to 2562 m in Beaver, Carbon, Daggett, Duchesne, Emery, Garfield, Grand, Iron, Juab, Kane, Millard, Piute, San Juan, Sanpete, Sevier, Tooele, Uintah, Utah, Washington, and Wayne counties; Nevada to Colorado, south to California, Arizona, New Mexico, Texas, and Mexico; 77 (xiii).

Var. *mojavensis* (Engelm. & Bigel.) L. Benson [*Cereus mojavensis* Engelm. & Bigel.]. Mixed desert shrub, pinyon-juniper, and ponderosa pine communities at 1550 to 2257 m in Beaver, Millard, and Washington counties; 3 (i).

FEROCACTUS Britt. & Rose

Plants hemispheric to cylindric, massive; ribs thick, prominent, somewhat spirally arranged; spines coarse, the central ones flattened and transversely annulate, not hooked; areoles large, more or less woolly when young; flowers subterminal, yellow, funnel-form; stamens numerous; ovary and floral tube scaly, not woolly; fruit oblong in outline, dry at maturity, dehiscent by a basal pore.

***Ferocactus acanthodes* (Lem.) Britt. & Rose** [*Echinocactus acanthodes* Lem.]. Plants mainly 2–15 dm tall and 2–5 dm thick or more; ribs 20–30; areole 1–1.5 cm long, brown-woolly when young; spines pink, red, or yellow, the central ones 1–4, subulate, flattened, annulate, curved, 4–8 cm long or more; radial spines with mixed coarse and slender ones; flowers 4–6 mm long, the scales of the tube and ovary overlapping when young, ovate; perianth segments oblong to spatulate; filaments yellow; fruit 3–3.5 cm long; seeds 2–3 mm long, reticulate. Limestone and dolomite outcrops and gravels at 760 to 1375 m in Washington County; Nevada, California, and Arizona; 1 (0). Our material belongs to **var. *lecontei* (Engelm.) Lindsay** [*Echinocactus lecontei* Engelm.]. This is the largest cactus native to Utah; it is distinguished from *Echinocactus polycephalus* by the large size, glabrous ovaries, and merely short-woolly areoles.

MAMMILLARIA Haw.

Subglobose to shortly cylindric plants, stems solitary or few; tubercles many, elon-

gate, in spiral rows; areoles spiniferous; spines smooth, the central 1–4 straight or 1 or more hooked; flowers borne between tubercles, diurnal; fruit fleshy, red, lacking appendages, elongate.

***Mammillaria tetrancistra* Engelm.** [*Phellosperma tetrancistra* (Engelm.) Britt. & Rose.]. Stems 4–10 cm tall or more, 4–6 cm wide; tubercles 4–10 mm long, more or less woolly in the axils when young; central spines 1–4, dark, 1 or more hooked, 10–15 mm long; radial spines 30–45, mostly whitish; flowers 25–30 mm long; sepaloids green with pink margins; petaloids rose to pink-purple; fruit scarlet, 12–20 mm long. Warm desert shrub communities at 760 to 1300 m in Washington County; Nevada, California, Arizona; 3 (ii).

NEOLLOYDIA Britt. & Rose

Subglobose to shortly cylindric plants, mostly solitary; ribbed and more or less tuberculate; areoles small; central spines 1 to several or lacking, straight (or curved), not hooked; radial spines 9–10; flowers borne subapically at the base of a woolly groove, purple or pink-purple; fruit green, drying tan, dehiscing by a basal pore, the scales and their axils glabrous.

***Neolloydia johnsonii* (Parryi) L. Benson** [*Echinocactus johnsonii* Parry in Engelm.; *Echinomastus johnsonii* (Parry) Baxter; *Ferocactus johnsonii* (Parry) Britt. & Rose]. Stems solitary, seldom branched, 8–20 cm tall, 5–10 cm thick, the ribs 17–21, obscured by interlocking spines; areoles with a short narrow woolly groove running to the axil; central spines pink to reddish or purplish, 3–4 cm long, terete; radial spines paler in color; flowers 5–6 cm long, purple or pink-purple; fruit green, drying tan, oblong, 10–15 mm long, nearly naked, splitting dorsally; seeds ca 2.5 mm long, papillate. Warm desert shrub community at 760 to 1250 m in Washington County; Nevada, Arizona, and California; 3 (i).

OPUNTIA Mill.

Stems jointed, the joints flattened, cylindric, or clavate; areoles with glochids (i.e., detachable barbed spinules), and commonly

with 1 or more stout spines (less commonly spineless); spines naked or sheathed; leaves terete, fleshy, caducous; flowers borne in areoles of previous year's growth, variously colored; floral tube cup shaped; ovary with areoles; stamens numerous; stigmas short; fruit fleshy or dry, armed or unarmed; seeds with a bony aril, flattened.

1.	Stem joints cylindric or clavate; spines with detachable epidermal sheaths, at least apically (subgenus <i>Cylindropuntia</i>)	2
—	Stem joints flattened; spines not sheathed (subgenus <i>Opuntia</i>)	5
2(1).	Stem joints clavate, 1 or few above ground, mainly 3–10 cm tall, arising from a tuberous subterranean joint; plants of Millard, Juab, and Tooele counties	<i>O. pulchella</i>
—	Stem joints cylindric, several to numerous above ground, mainly 3–20 dm tall, not arising from a tuberous joint; plants of various distribution	3
3(2).	Joints mainly less than 2 cm thick; fruits fleshy at maturity; plants of rather broad distribution in Utah	<i>O. whipplei</i>
—	Joints mainly over 2.5 cm thick; fruits dry at maturity; plants mainly of Washington County	4
4(3).	Ridge of tubercle on mature joints mainly 18–22 mm long, more than 3 times longer than broad; longer terminal joints mainly more than 15 cm long	<i>O. acanthocarpa</i>
—	Ridge of tubercle on mature joints mainly 10–15 mm long, only 1–2 times longer than broad; longer terminal joints mainly shorter than 15 cm long	<i>O. echinocarpa</i>
5(4).	Areoles with glochids only; spines not developed (except in hybrids with other taxa), or if present the glochids very numerous and 4–10 mm long; plants of Washington, Kane, and San Juan, and less commonly of Emery, Garfield and Wayne counties	<i>O. basilaris</i>
—	Areoles with glochids and spines, at least some, or if lacking (a condition probable in all species) then of different distribution	6
6(5).	Fruit dry at maturity, finally tan, green or reddish when young; seeds mainly 4–8 mm long, rough and irregular in outline (key nonfruiting specimens both ways)	7
—	Fruit fleshy at maturity, red or reddish purple to purple; seeds mainly 2.5–4.5 mm long, smooth and regular in outline	10
7(6).	Largest joints 2–8 cm long, 1.5–3.5 cm wide, readily detachable (carried burrlike by animals)	<i>O. fragilis</i>
—	Largest joints mainly 7–15 cm long or more, 4–12 cm broad or more, not readily detachable	8
8(7).	Spines not especially flattened, even basally, terete or nearly so, or rarely lacking; plants transitional to the next	<i>O. polyacantha</i>
—	Spines at least somewhat flattened, at least basally, usually elliptic in cross-section	9
9(8).	Spines less than 1 mm thick, more or less flexible; joints mainly 5–15 cm long and 3–10 cm wide; plants rather widespread, transitional to the next	<i>O. erinacea</i>
—	Spines over 1 mm thick (at least some), not especially flexible; joints often over 15 cm long and 10 cm wide; plants of the Glen Canyon vicinity (transitional to <i>O. phaeacantha</i>)	<i>O. nicholii</i>

- 10(9). Spines terete to subterete, not flattened (except when hybridizing with *O. phaeacantha*), commonly 1–6 per areole 11
- Spines at least basally flattened, narrowly elliptic in cross-section, commonly 3 per areole 12
- 11(10). Spines gray or brownish; plants usually prostrate, not forming upright clumps; largest joints mainly less than 12 cm long; plants scattered in Utah *O. macrorhiza*
- Spines tan or variously colored; plants usually upright and with several joints standing above the ground; largest joints mainly more than 12 cm long; plants of San Juan and Washington counties *O. littoralis*
- 12(10). Joints subcircular in outline; spines all deflexed, yellow; plants of Washington County *O. chlorotica*
- Joints mainly obovate in outline; spines spreading in various directions, brown to tan or gray; plants of rather broad distribution *O. phaeacantha*

Opuntia acanthocarpa* Engelm. & Bigel.** Shrubs, mainly 8–15 dm tall or more; trunk short; larger terminal joints mostly 12–50 cm long, 2–3 cm thick; tubercles decurrent along the joint, mostly 15–50 mm long and 4–6 mm wide; leaves caducous; areoles circular; spines 6–20 or more per areole, 1–4 cm long, variously colored, the sheathes straw colored; glochids minute; flowers 4–6 cm long; sepals greenish yellow; petaloids red, purplish, or yellow; ovary spiny; fruit dry, tan or brown, spiny, 2–4 cm long; seeds 5–8 mm long, tan or whitish. Larrea-Joshua tree, and other warm desert shrub communities at 760 to 1220 m in Washington County; Nevada, California, Arizona, and Mexico; 5 (i). Two varieties are reported from Utah by Benson (1982); **var. *acanthocarpa, with tubercular ridges 30–50 mm long and longer joints 25–50 cm long; and **var. *coloradoensis* L.**

Benson, with tubercular ridges 15–22 mm long and larger joints 12–30 cm long. More material is necessary to determine the nature of the Utah materials.

***Opuntia basilaris* Engelm. & Bigel.** Plants mainly 10–30 cm high and to 1 m broad or more; joints blue, blue-green, violet-green, or green, obpyriform, obovate, orbicular, or spatulate, 5–30 cm long, 2.5–12 cm broad; areoles circular, 9–17 mm apart; spines lacking (some present in various hybrids); glochids brown to tan; flowers 5–8 cm long; sepals greenish, edged with violet or yellow; petaloids violet or yellow; fruit 2.5–3 cm long, dry at maturity, green, becoming tan or gray; seeds ca 6–8 mm long, white or grayish. Four more or less distinctive and geographically correlated, but problematical, varieties are present.

1. Joints obpyriform, seldom otherwise, suffused with violet or blue; glochids brown; plants of Washington and San Juan counties *O. basilaris* var. *basilaris*
- Joints mainly obovate to spatulate, suffused with blue, or green or yellow; glochids tan to yellowish; plants variously distributed 2
- 2(1). Spines often present; glochids mainly 4–10 mm long, often copious; plants of Washington County, transitional to *O. phaeacantha* *O. basilaris* var. *woodburyi*
- Spines lacking or essentially so; glochids seldom to 4 mm long, moderately abundant; plants of various distribution 3
- 3(2). Joints obovate, bluish green (drying ashy or bluish); flowers commonly yellow; plants of Kane and Washington counties *O. basilaris* var. *aurea*
- Joints spatulate, yellowish to bluish green; flowers commonly violet; plants of Emery, Garfield, and Wayne counties *O. basilaris* var. *heilii*

Var. *aurea* (Baxter) W. T. Marshall [*O. aurea* Baxter, type from Pipe Springs, Arizona]. Sagebrush, pinyon-juniper, and ponderosa pine communities at ca 1220 to 2075

m in Kane and Washington counties; Arizona; a Plateau endemic; 6 (iii). Intermediates occur between this taxon and *O. erinacea* and *O. polyacantha*.

Var. *basilaris*. Warm desert shrub community at 760 to 1770 m in San Juan (Cataract Canyon) and Washington counties; Nevada, California, Arizona, and Mexico; 10 (iv). The materials from Cataract Canyon differ in tenuous ways from the typical material in Washington County; they do not seem worthy of taxonomic recognition.

Var. *heilii* Welsh & Neese. Salt desert shrub communities at 1460 to 1680 m in Emery, Garfield, and Wayne counties; endemic; 3 (0).

Var. *woodburyi* Earl. Warm desert shrub community at ca 920 m in Washington County (type from Fort Pierce Wash); endemic; 4 (i). This "variety" appears to have been derived from introgression involving *O. basilaris* var. *basilaris* and *O. phaeacantha*, which are sympatric at the type locality (N. D. Atwood, pers. comm.). The plants are long lived and form a portion of the diversity within the opuntias of Washington County. Recognition at taxonomic rank is problematical for two reasons; naming of hybrid derivatives could proceed endlessly, and the dilemma of placement of the "variety" in one of the parental species begs the question of the contribution of the other parent (i.e., it is allied to both, but it cannot be placed in both).

***Opuntia chlorotica* Engelm. & Bigel.** Shrubby plants, mainly 6–15 dm tall; trunk to 30 cm long; larger joints 15–20 cm long and about as broad, orbicular to suborbicular, blue-green; areoles elliptic, ca 20 mm apart; spines present in all but basal areoles, yellowish, 1–6, all deflexed, straight or curved at the base, 2.5–4 cm long; glochids yellow; flowers 5–8 mm long; sepals and petaloids yellow, or suffused with red; ovary with glochids and some spinules; fruit fleshy, grayish, tinged with purple, lacking spines; seeds 2.2–3 mm long, tan, smooth. Desert shrub communities at 1400 m in Washington County (Beaverdam Mts. and Zion Canyon); Nevada, California, Arizona, New Mexico, and Mexico; 3 (ii).

***Opuntia echinocarpa* Engelm. & Bigel.** Shrubs, mainly 8–15 dm tall; trunk to half of plant height; larger terminal joints mainly less than 15 cm long (5–15), 2–4 cm thick; tubercles decurrent along the joint, mostly

6–15 mm long and 4–5 mm wide; leaves caducous; areoles circular; spines 3–12 per areole, 1–3 cm long, straw colored or silvery or yellow; sheaths colored like the spines; glochids minute; flowers 3–4.5 cm long; sepals and petaloids greenish yellow, the outer sometimes suffused reddish; fruit dry, green, turning tan. Creosote bush, Joshua tree, blackbrush, and shadscale communities at 760 to 1376 m in Beaver (?) and Washington counties; Nevada, California, Arizona, and Mexico; 5 (iii).

***Opuntia erinacea* Engelm.** Plants mainly 10–30 cm tall and to 1 m in diameter or more; larger joints obovate to spatulate, glaucous, 5–19 cm long, 3–11 cm wide; areoles small, 4–18 mm apart; spines at all or most areoles or only in the upper ones (or lacking?), 4–9 per areole, deflexed, flexible, straight or irregularly curved, 0.5–10 cm long, less than 1 mm thick, at least some clearly flattened (at least basally); glochids yellow to tan or brown; flowers 4.5–7.5 cm long; sepals commonly greenish; petaloids yellow, bronze, pink, or violet; ovary usually spiny; fruit dry, tan to brown, spiny, 2.5–3 cm long, deciduous; seeds 4–6 mm long, whitish. Plants of this complex of morphologically differing forms intergrade freely among themselves, and they hybridize with the dry fruited *O. basilaris* var. *aurea*, *O. fragilis*, *O. nicholii*, and with the varieties of *O. polyacantha*. Further, they hybridize with the fleshy fruited *O. phaeacantha*, *O. littoralis*, and likely with *O. macrorhiza*. Intergradation with *O. polyacantha* is sufficiently complete as to pose the question of whether maintenance of the proposed segregates within separate species is reasonable. I follow tradition in maintaining them thusly, because, if a case is made for combining these two species, then a similar case must be considered for union of all platyopuntias with which they intergrade into a single polymorphic species. The variants could then be recognized as belonging to numerous infraspecific taxa, approximately equal to the number of taxa recognized currently. Such a proposal would solve none of the basic problems resulting from intergradation of taxa, despite the convenience of having only one name at the specific level for all of the prickly pears. Three varieties are recognized.

1. Spines lacking in much of the joint, mainly confined to the upper half or along the upper edge; plants widespread *O. erinacea* var. *utahensis*
- Spines present in much or all of the joint; plants of the southern half of Utah 2
- 2(1). Spines stiff, rigid, the longest mainly 1–4 cm long; plants widespread in southern Utah *O. erinacea* var. *erinacea*
- Spines slender and more or less flexible, the longest 3–10 cm long; plants of Washington County *O. erinacea* var. *ursina*

Var. *erinacea* [*O. hystericina* sensu Utah authors]. Warm and mixed desert shrub communities at 885 to 1285 m in Beaver, Emery, Grand, Kane, Millard, San Juan, Washington, and Wayne counties; Nevada to Colorado, California, Arizona, and New Mexico; 20 (ix). It has been postulated (Benson 1982) that this phase of *O. erinacea* is one of the putative parents of *O. nicholii*, the other being *O. phaeacantha*. Along Glen Canyon there are many specimens which bridge this variety with *O. nicholii*.

Var. *ursina* (Weber) Parish [*O. ursina* Weber; *O. rubrifolia* Engelm. ex Coulter, type from St. George]. Warm desert shrub community at 760 to 900 m in Washington County; Nevada, California, and Arizona; 4 (ii). Our material shows evidence of mixing with var. *erinacea*.

Var. *utahensis* (Engelm.) L. Benson [*O. sphaerocarpa* var. *utahensis* Engelm.; *O. rhodantha* K. Schum.; *O. xanthostemma* K. Schum.; *O. erinacea* var. *xanthostemma* (K. Schum.) L. Benson]. Blackbrush, pinyon-juniper, sagebrush, mountain brush, ponderosa pine, and aspen communities at 1220 to 2810 m in most if not all Utah counties; Idaho to California, Arizona, New Mexico, and Wyoming; 29 (xiii). This variety is the counterpart of *O. polyacantha* var. *polyacantha*, with which it hybridizes wherever they meet.

***Opuntia fragilis* (Nutt.) Haw.** [*Cactus fragilis* Nutt.; *O. fragilis* var. *denudata* Wiegand & Backeburg; *O. brachyarthra* Engelm. & Bigel.; *O. fragilis* var. *brachyarthra* (Engelm. & Bigel.) Coult.]. Plants mat forming, mainly 5–10 cm tall and to 5 dm wide; larger joints 2.5–7 cm long, 1–4 cm wide, obovate to ovate or orbicular to elliptic in outline, blue-green, often to half as thick as wide or more, readily detached and transported by animals; leaves caducous; areoles 3–12 mm apart; spines in most areoles or only in the upper ones or sometimes lacking,

1–9 per areole, disoriented, 4–25 mm long or more, terete to somewhat flattened; glochids tan to brown; flowers 3.5–6 cm long; sepaloids greenish; petaloids yellowish, greenish, bronze, or violet; fruit dry, tan, spiny or spineless, 1.2–2.5 cm long. This is a taxon of unusually great latitude of habitat types ranging from low elevation marshlands and riparian sites upwards to pinyon-juniper, ponderosa pine, sagebrush, mountain brush, and aspen communities at 1370 to 2565 m in Box Elder, Carbon, Duchesne, Emery, Garfield, Piute, San Juan, Sanpete, Sevier, Uintah, Utah, and Weber counties; British Columbia to Ontario, south to California, Nevada, Arizona, New Mexico, Texas, and Iowa; 18 (iii). Morphological amplitude of our specimens is greater than that reported for the species as a whole (Benson 1982), excluding hybrids presumably intermediate with both *O. erinacea* and *O. polyacantha*. Recognition of proposed infraspecific taxa seems moot.

***Opuntia littoralis* (Engelm.) Britt. & Rose** [*Opuntia engelmannii* var. *littoralis* Engelm.]. Plants mainly 30–50 cm high and 0.5–1.2 m wide, more or less sprawling; larger joints 10–18 cm long, 7–14 cm wide, obovate to orbicular, green or glaucous; areoles mainly 15–30 mm apart; spines in all, or only in the upper, areoles, 1–6 per areole, mainly 2–7 cm long, spreading to deflexed, straight or curved, terete to somewhat flattened; glochids yellowish to brown; flowers 5–7.5 cm long; sepaloids greenish; petaloids yellow, the bases sometimes violet or rose-purple; fruit fleshy, reddish or purplish-red, armed with glochids, 3–6 cm long; seeds 3–6 mm long, tan or gray. Pinyon-juniper community (?) in Washington and San Juan counties (reported by Benson 1982); Nevada, California, and Arizona; 1 (0). This plant can be mistaken for *O. phaeacantha*, with which it is at least partially sympatric. Our material is assigned to var. *martiniana* (L. Benson) L. Benson [*O. eriocentra* var. *martiniana* L. Benson].

***Opuntia macrorhiza* Engelm.** [*O. utahensis* J. A. Purpus; *O. compressa* Macbr.]. Plants mainly 7–15 cm high and 2–15 dm wide or more; larger joints 5–12 cm long, 5–7.5 cm wide, obovate to orbicular, glaucous; leaves caducous; spines mainly in upper areoles, 1–6 per areole, commonly deflexed, straight or slightly curved, 1.5–5 cm long, terete or somewhat flattened; glochids yellow to brown; flowers 5–6.5 cm long; sepals greenish or reddish; petals yellow or tinged reddish basally; ovary smooth at anthesis, with few areoles; fruit fleshy, purple or purplish, with some glochids, 2.5–5 cm long; seeds 4–5 mm long, tan or gray. Pinyon-juniper and mountain brush communities in Garfield, Kane, Salt Lake, San Juan, and Washington counties, the reports mainly by Benson (1982); Idaho to Wisconsin, south to Mexico, Texas, and Louisiana; 3 (0). This is mainly a plains species, with extensions into Utah where some of the reports might represent recent introductions. The similar *O. humifusa* (Raf.) Raf. is reported for Utah on the basis of a collection from Utah County (Mason 6570 US), which was taken from along a railroad right-of-way. It is distinguished by having green joints and spines 1 per areole.

***Opuntia nicholii* L. Benson.** Plants mainly 15–25 cm high and 0.5–2 m wide or more; larger joints 10–20 cm long and 5–12 cm wide, narrowly obovate to obovate, bluish-green; areoles 10–20 mm apart; spines usually in all areoles, 4–7 per areole, deflexed, often twisted and curving, mainly 5–12 cm

long, flattened, some more than 1 mm thick; glochids yellow or tan; flowers 6–7 (8) cm long; sepals green, edged with purple or yellow; petals violet or yellow; fruit dry, tan to brown, 2.5–3.5 cm long, more or less spiny; seeds 7–8 mm long, whitish. Salt desert shrub and warm desert shrub communities at 1200 to 1500 m in Garfield, Kane, and San Juan counties (where it grows along Glen Canyon); Arizona; a Plateau endemic; 2 (i). Evident intermediates between *O. nicholii* and both *O. erinacea* var. *erinacea* and *O. phaeacantha* are known. Benson (1982) postulates a hybrid origin for this entity, and states that it should probably best be treated at varietal rank, but with which species?

***Opuntia phaeacantha* Engelm.** Plants 30–90 cm high and 3–15 dm wide or more; larger joints 10–40 cm long, 7–25 cm wide, obovate to suborbicular, bluish green; areoles mainly 20–34 mm apart; spines in most areoles or restricted to upper ones or along the margin, or none, 1–9 per areole, spreading or deflexed, 2–8 cm long, flattened at least basally in some; glochids brown, reddish, or tan; flowers 6–7.5 cm long; sepals greenish, edged yellow or red; petals yellow, or suffused with red below; ovary spineless, but with glochids; fruit fleshy, purple to red-purple, 3.5–8 cm long; seeds 4–5 mm long, tan to gray. Three intergrading varieties have been identified from Utah (Benson 1982); their recognition at taxonomic rank is questionable, at least as far as our specimens are concerned.

- 1. Larger joints 10–15 cm long and 7–10 cm wide; plants of Washington and San Juan counties *O. phaeacantha* var. *phaeacantha*
- Larger joints 12–40 cm long and 9–25 cm wide; plants of various distribution 2
- 2(1). Joints mainly 12–20 cm long and 9–15 cm wide; plants rather broadly distributed in southern Utah *O. phaeacantha* var. *major*
- Joints mainly 20–40 cm long and 15–25 cm wide; plants of San Juan and Washington counties *O. phaeacantha* var. *discata*

Var. *discata* (Griffiths) Benson & Walkington [*O. discata* Griffiths]. Warm desert shrub, pinyon-juniper, and sagebrush communities at 905 to 1800 m in San Juan (White Canyon, associated with prehistoric Indian dwellings) and Washington counties; California to Texas and Mexico; 3 (ii).

Var. *major* Engelm. Warm desert shrub, pinyon-juniper, and mountain brush communities in Garfield, Kane, San Juan, and Washington counties; Nevada to Kansas, south to California, Mexico, and Texas; 12 (iii). This is the common phase of the species in Utah; plants north of the southern tier of counties

having fleshy fruit probably belong to *O. macrorhiza*, with which transitional forms are known.

Var. *phaeacantha*. This variety is reported by Benson (1982) from Washington County; Arizona, Colorado, New Mexico, Texas, and Mexico; 0 (0).

***Opuntia polyacantha* Haw.** Plants mainly 5–20 cm high and 3–30 dm wide or more; larger joints 5–15 (20) cm long (rarely longer) and 4–12 cm wide, obovate to orbicular, bluish green, not readily detached; areoles mainly 5–15 mm apart; spines variously borne in some or all areoles or lacking, often 6–10 per areole, variously oriented (all erect or spreading or some or all deflexed), straight or curved, terete (or somewhat flattened); glochids yellowish or tan; flowers 5–8 cm long; sepals green, margined with yellow or red; petals yellow, bronze, or pink to

violet; ovary with glochids and often with spines; fruit dry, 2–4 cm long, spiny, tan or brownish, deciduous; seeds 3–6 mm long, tan to white. This species, along with *O. erinacea*, forms a plexus around which revolve all other species of subgenus *Opuntia* (the platyopuntias) in Utah. Members of this complex form hybrids with *O. fragilis*, *O. erinacea*, *O. basilaris*, and *O. phaeacantha*. Those, in turn, are transitional to all other species. Diversity of form and joint size; spine length, number, size, cross-sectional shape, and color; flower size and color; and other features give indications of genetic variability, differential response to ecological situations, and of problems of interpretation. Four varieties from Utah are treated by Benson (1982); they are more or less sympatric and intergrading.

1. Spines slender, flexible and curving, often whitish; plants of Grand and San Juan counties *O. polyacantha* var. *trichophora*
- Spines slender to coarse, not flexible (penetrating the skin before collapsing), mostly straight, or sometimes lacking; plants of various distribution 2
- 2(1). Spines mainly in upper areoles; fruits sparingly spiny; plants mainly of the eastern tier of counties *O. polyacantha* var. *juniperina*
- Spines in most areoles, or if less abundant or lacking in the lower ones then often of other distribution; fruits often spiny 3
- 3(2). Spines in lower areoles mainly less than 12 mm long, those of upper areoles mainly less than 4 cm long, or spines lacking *O. polyacantha* var. *polyacantha*
- Spines in lower areoles mainly over 12 mm long, those of upper areoles often over 4 cm long *O. polyacantha* var. *rufispina*

Var. *juniperina* (Britt. & Rose) L. Benson [*O. juniperina* Britt. & Rose]. Desert shrub and pinyon-juniper communities at ca 1400 to 2000 m in Grand, San Juan, and Uintah counties; Wyoming to Colorado, New Mexico, and Arizona; 3 (i). As far as specimens from Utah are concerned this taxon could pass under var. *polyacantha* without adding much to the variation of the expanded typical variety. The coarser spines in fewer upper areoles have been considered as definitive.

Var. *polyacantha* [*O. polyacantha* var. *watsonii* Coult., type presumably from Summit County]. Salt Desert shrub, mixed desert shrub, pinyon-juniper, sagebrush, mountain brush, mixed conifer, and aspen communities at 1370 to 2565 m in probably all Utah counties; British Columbia to Saskatchewan, south

to Nevada, New Mexico, and Oklahoma; 36 (iv). This variety is transitional with the former and the next.

Var. *rufispina* (Engelm. & Bigel.) L. Benson [*O. missouriensis* var. *rufispina* Engelm. & Bigel.]. Blackbrush, mixed desert shrub, and pinyon-juniper communities at 1370 to 2200 m in Carbon, Emery, Garfield, Grand, Kane, Millard, San Juan, Washington, and Wayne counties; Wyoming to Nevada and California, south to Arizona and Texas; 21 (iii). This assemblage seems not to represent plants with genetic affinities. Rather the specimens appear to be artificial aggregations of phenotypically similar individuals. The use of spine characteristics as diagnostic results in a dilemma; the assemblage thus defined should be allied genetically to be recognized at a taxonomic level, but the definition

is faulty. Thus, those plants of the Colorado drainage system show evidence of derivation from hybridization with *O. erinacea*; the plants of the Great Basin do not.

Var. *trichophora* (Engelm. & Bigel.) Coult. [*O. missouriensis* var. *trichophora* Engelm. & Bigel.]. Desert shrub and pinyon-juniper communities at 1125 to 1250 m in Grand, Kane, and San Juan counties; Colorado, Arizona, and New Mexico, Oklahoma, and Texas; 6 (iv).

***Opuntia pulchella* Engelm.** Sand Cholla. Plants mainly 3–10 cm tall and about as broad, arising from an areolate glochid-armed tuberous joint 2–7 cm thick or more; joints mainly 1–5 cm long and 0.6–1.5 (2) cm thick, clavate to cylindric, green or blue-green; tubercles 5–9 mm long and 4–5 mm wide; areoles spineless or with the upper mainly spiniferous, 8–15 per areole, straight or curved, 1–3.5 cm long or more, strongly flattened, the epidermal sheath not at all or poorly developed; glochids yellow to brown; flowers 3–4.5 cm long; sepals green, margined with pink-purple; petals purple to violet; fruit 2–3 cm long, fleshy, red, prominently areolate and spiny; seeds 3–4.5 mm long, whitish. Salt and mixed desert shrub communities at 1430 to 1770 m in Juab, Millard, and Tooele counties; Nevada; a Great Basin endemic; 8 (iv). This taxon was named three times from Utah, all of the names based on types taken from the Desert Experimental Range in western Millard County, i.e., *Micro-puntia brachyropalia* Daston, *M. barkleyana* Daston, and *M. spectatissima* Daston. All are characteristic of the species as it occurs in Utah, and none are worthy of taxonomic consideration.

***Opuntia whipplei* Engelm. & Bigel.** Plants low shrubs or less commonly mat-forming, mainly 10–60 cm tall or more; larger joints 2–15 cm long and 1–2 (2.5) cm thick; tu-

bercles 8–9 mm long, 3–5 mm wide; leaves caducous; spines 4–10 or more per areole, straight, mainly 0.6–3 cm long, subulate to flattened; glochids yellow to tan or whitish; flowers 2–4 cm long; sepals and petals yellowish or yellowish green; fruit fleshy, 2–3 cm long, yellow, glochidiate; seeds 2.5–3 mm long, tan. Desert shrub-grass and pinyon-juniper communities at 1340 to 1895 m in Beaver, Iron, Kane, Millard, and Washington counties; Nevada, Colorado, Arizona, and New Mexico; 15 (x). Our material belongs to var. *whipplei*. Specimens with short terminal joints have been regarded tentatively as var. *multigeniculata*, but they fit in a graded series with *O. whipplei* in a strict sense. Dwarf plants at the limits of their ecological tolerance seem to represent a “cactus-line,” corresponding to the dwarf conifers at “timberline.” This seems to be the case with *O. whipplei* at the northern margin of its distribution in southwestern Millard County. A taxon represents the sum of its characteristics, not merely those considered to be diagnostic. *O. multigeniculata* Clokey is evidently restricted to the Spring (Charleston) Mountains and vicinity in southern Nevada.

PEDIOCACTUS Britt. & Rose

Plants globose to depressed-hemispheric, solitary; tubercles spirally arranged; areoles woolly, at least when young, with spines various but not hooked; flowers subterminal, borne on one side of the areole at the tubercle apex, small; sepals shorter than the petals; fruit dry, green, becoming tan to brownish or yellowish, naked or scaly, dehiscent by a vertical slit; seeds black tuberculate.

HEIL, K., B. ARMSTRONG, AND D. SCHLESER. 1981. A review of the genus *Pediocactus*. *Cactus & Succ. J. (U.S.)* 53: 17–39.

1.

Central spines 1–7, 6–30 mm long or more

2
- Central spines lacking, the longest lateral spines mainly less than 6 mm long

3
- 2(1).

Longest spines mainly 12–25 mm long; sepals long-fimbriate; plants known only from gypsiferous substrates in Washington and Kane counties

P. sileri
- Longest spines mainly 6–12 mm long; sepals subentire or shortly fimbriate; plants broadly distributed, seldom as above

P. simpsonii
- 3(1).

Longest spines 4 mm long or less, white, or lacking, often obscured by a dense mat of persistent white hairs; flowers peach to pink; plants of western Wayne County

P. winkleri

Longest spines more than 4 mm long, pale yellowish, not obscured by hairs, the woolly hairs pale yellowish and caducous; flowers yellow to bronze or peach; plants of north central Emery County *P. despainii*

***Pediocactus despainii* Welsh & Goodrich**

Plants solitary or less commonly colonial, subglobose to depressed-hemispheric, 3.8–6 cm tall, 3–9.5 cm wide; tubercles 6–10 mm long, 5–11 mm wide; areoles elliptic, persistently white-woolly, the central spines lacking; radial spines 9–13, 1.7–6 mm long, pale yellowish; flowers 1.5–2.5 cm long, 1.8–2.5 cm wide; petaloids yellow-bronze to bronze or pinkish; fruit green, drying reddish brown, smooth, obovoid, 9–11 mm long, 10–12 mm wide; seeds shiny black, papillate to ridged, 3–3.5 mm long. Open pinyon-juniper community on limestone gravels at ca 1830 m in Emery County; endemic; 5 (0).

***Pediocactus sileri* (Engelm.) L. Benson**
Gypsum Cactus. [*Echinocactus sileri* Engelm. in Coult.; *Utahia sileri* (Engelm.) Britt. & Rose]. Plants solitary (less commonly colonial), depressed-hemispheric to cylindroid, 5–25 cm high, 6–12 cm wide; tubercles 9–15 mm long, 6–11 mm wide; areoles circular, persistently white-woolly; central spines 3–7, 13–30 mm long, blackish brown when young, straight; radial spines 11–15, 11–21 mm long, white; flowers 18–22 mm long, 20–30 mm wide; petaloids yellow or yellowish with purple veins; sepaloids conspicuously fringed; fruit dry, greenish yellow, 1.2–1.5 cm long; seeds gray to black, 3.5–5 mm long. Salt desert shrub community at ca 900 to 1590 m in Kane and Washington counties; Arizona; a Plateau endemic; 1 (i). The type locality for this remarkable species is Pipe Springs, Arizona, but those springs were thought by early collectors to be in Utah, hence the name *Utahia*, which commemorates an Arizona type.

***Pediocactus simpsonii* (Engelm.) Britt. & Rose** [*Echinocactus simpsonii* Engelm.; *P. hermannii* W. T. Marshall, type from near Hatch; *E. simpsonii* var. *minor* Engelm.; *P. simpsonii* var. *minor* (Engelm.) Cockerell]. Stems solitary or colonial, depressed-hemispheric to subglobose, 2–15 cm high, 3–20 cm wide (or more); tubercles 5–25 mm long, 4–7 mm wide; areoles elliptic to subcircular; central spines (1–3) 4–10, mainly 5–25 mm long, brownish or blackish; radial spines mainly

10–25, white; flowers 1.2–3 cm long; petaloids whitish, pinkish, yellowish or greenish; sepaloids shortly fimbriate; fruit green, often turning reddish brown, with few scales, 6–11 mm long, 5–10 mm wide; seeds gray to black, tuberculate, 2–3 mm long. Shadscale, mixed desert shrub, pinyon-juniper, sagebrush, and Douglas fir communities at 1460 to 2830 m in Beaver, Box Elder, Carbon, Duchesne, Emery, Garfield, Grand, Juab, Piute, San Juan, Sevier, Tooele, Utah, Washington, and Wayne counties; Washington to Wyoming, south to Nevada, Arizona, and New Mexico; 26 (viii). Segregation of this common species of cactus into varieties seems not to be practical or even possible for Utah materials. Ridge tops in some south central mountains and plateaus support one to several plants per square foot, mainly flush with the ground surface.

***Pediocactus winkleri* Heil.** Plants solitary or sometimes colonial, 3.9–6.8 cm tall, 2.7–5 cm wide; tubercles 4–7 mm long, 5–7 mm wide; areoles elliptic, persistently white-woolly; central spines lacking; radial spines 8–14, 1.5–4 mm long, white; flowers 1.7–2.2 cm long, 1.7–3 cm wide; petaloids peach to pink; sepaloids like the petaloids, except the outer darker; fruit green, drying reddish brown, smooth, obovoid, 7–10 mm long, 8–11 mm wide; seeds shiny black, papillate to ribbed, 2.5–3 mm long. Salt desert shrub communities at 1460 to 1590 m in Wayne Co.; endemic; 5 (0). This is a remarkable tiny plant of poor quality, saline, fine-textured substrates.

SCLEROCACTUS Britt. & Rose

Plants subglobose, depressed-hemispheric, ovoid, obovoid, or cylindroid; ribs 8–17; tubercles coalescent; areoles circular to elliptic; central spines 0 or 1–10, usually 1 or more hooked, or all straight; radial spines 2–15, straight; flowers subterminal, borne on upper side of tubercle adjacent to the areole, the scar persisting; floral tube short; petaloids pink to violet, white, or yellow; fruit dry, green turning reddish to tan, naked or with

scales, dehiscent by basal and horizontal or lateral and vertical slits; seeds black, papillate-reticulate. NOTE: The taxonomy of this

genus is subject to interpretation because of the remarkable diversity of form present in each of the species complexes.

- 1. Plants depressed-hemispheric to subglobose; areoles retaining juvenile pubescent radial spines for some years, finally with 1 or 2 hooked central spines; plants of the Great Basin *S. pubispinus*
- Plants variously shaped, but if as above and with areoles retaining juvenile radial spines for several years, then the spines glabrous and plants not of the Great Basin 2
- 2(1). Flowers mostly 2–3 cm long and broad; yellowish, pink, or white with pale pink midrib dorsally; juvenile condition retained for several years; plants of Emery and Wayne counties *S. wrightiae*
- Flowers mostly 3.5–5 cm long and broad, rose pink to violet, white, or yellow; plants of broad distribution in eastern Utah *S. whipplei*

Sclerocactus pubispinus (Engelm.) L. Benson [*Echinocactus pubispinus* Engelm.]. Plants solitary or sometimes colonial, depressed-hemispheric to ovoid, 1–10 cm high, 2–15 cm wide; ribs 6–13; tubercles more or less developed; areoles circular to elliptic; juvenile spines and often the others (in part) densely or sparingly white-pubescent, finally glabrate; central spines lacking or 1–5, the lower one often hooked, 1–3 cm long, the upper one flattened, 5–35 mm long, 0.7–2.2 mm wide; radial spines 5–12, spreading; flowers 2.5–3.5 cm long; sepals bronze to brownish; petals yellow, bronze, pink, or violet to rose-purple; fruit dry, green or pink becoming tan to brownish, ellipsoid to obovoid, opening by vertical slits; seeds 2.8–3.4 mm long, papillate, black. This species was named simultaneously in 1863 as *Echinocactus pubispinus* and as *E. whipplei* var. *spinosior*. The type of the former was taken in Pleasant Valley, Juab County, Utah, or in adjacent White Pine County, Nevada (the boundary bisects the valley), and that of the

latter was taken in the Dugway or Thomas ranges in central northern Juab County. Both remained obscure for almost a century, with *S. pubispinus* being ignored and var. *spinosior* being placed with *S. whipplei* and interpreted as including what now belongs in var. *intermedius* of that species (sensu stricto, which it resembles in its broad upper central spines). The type of *S. pubispinus* is a juvenile plant lacking both flowers and fruit; that of var. *spinosior* consists of flowers and seeds. Modern interpretations are based on interpolations of presumed collection localities with known modern occurrences of these dwarf cacti. In a way these peculiar cacti share characteristics of *S. polyancistrus* (Engelm. & Bigel.) Britt. & Rose of southern Nevada (pubescent spines and the tendency to flattened upper central spine) and with *S. whipplei* (the flattened upper central spine). The smaller flowers and depressed growth form are diagnostic from both. There are two intergrading and partially sympatric varieties present.

- 1. Flowers rose to violet; widest upper central spines 1–2.2 mm wide
..... *S. pubispinus* var. *spinosior*
- Flowers bronze to yellow; widest upper central spines 0.7–1 mm wide
..... *S. pubispinus* var. *pubispinus*

Var. *pubispinus* Shadscale, sagebrush, winterfat, rabbitbrush, and pinyon-juniper communities on calcareous and dolomitic gravels and outcrops at 1800 to 1955 m in Beaver, Box Elder, Iron, Juab, Millard, and Tooele counties; Nevada; a Great Basin endemic; 13 (vi).

Var. *spinosior* (Engelm.) Welsh comb. nov. [based on: *Echinocactus whipplei* var. *spinosior* Engelm. Trans. Acad. Sci. St. Louis 2: 199. 1863; *S. spinosior* (Engelm.) Woodruff & Benson]. Shadscale, rabbitbrush, sagebrush, and pinyon-juniper communities on calcareous and igneous gravels and clay silts at

1525 to 1985 m in Beaver, Juab, Millard, and Sevier counties; Arizona (?); 15 (xi). The range of this variety is partially sympatric with var. *pubispinus* in western Beaver County and intermediates are known. The population from Sevier County differs in subtle ways from the remainder of the taxon, but does not seem to be worthy of taxonomic rank.

Sclerocactus whipplei (Engelm.) Britt. & Rose [*Echinocactus whipplei* Engelm. & Bigel.]. Plants solitary or in small colonies, depressed-hemispheric, obovoid, ovoid, or cylindrical, 5–35 cm tall or more, 5–15 cm thick; ribs mainly 8–15, tuberculate; central spines

1–4, the lower one (sometimes 2–4) hooked or all straight, mainly 1–7.5 cm long, curved or some or all of them straight, the upper central spine (at least) usually pale and flattened to flat and ribbonlike, 1–5 cm long or more, 0.7–3.5 mm wide, erect; radial spines 7–12 or more; flowers 3.5–5 cm long; sepals greenish, margined with rose purple, pink, white, or yellow; petals pink, violet, white, or yellow; fruit dry, green, becoming tan, sparingly scaly, 1.2–2.5 cm long; seeds 2–3.4 mm long, black, papillate. Two intergrading varieties are recognizable among our Utah materials.

1. Central spines all straight or essentially so; plants commonly of terrace gravels at lower elevations in the Uinta Basin and rarely elsewhere *S. whipplei* var. *glaucus*
Central spines hooked, at least the lowermost; plants of broad distribution, transitional to the above in the Uinta Basin *S. whipplei* var. *roseus*

Var. *glaucus* (J. A. Purpus) Welsh comb. nov. [based on: *Echinocactus glaucus* J. A. Purpus ex K. Schum. Gesamt. Kakteen. 438. 1898]. Salt desert shrub and shrub-grass communities on terrace gravels and less commonly on clays of the Uinta Formation at ca 1430 to 1770 m in Duchesne and Uintah (and San Juan?) counties; Colorado; 17 (ix). Plants with straight spines have long been known, and have been recognized as belonging to this genus. Their status has been open to question, because they differ in no other discernible way from the body of the species. Also, there is a question as to whether all of the straight-spined plants in Utah (e. g., Welsh et al. 21187 BRY) and in central western Colorado constitute “a taxon.” Instead, could they not be merely similarly derived evolutionary end lines arrived at quite independently? The intergradation of the Utah materials with the species suggests such a derivation, and the Uinta Basin material might be more closely allied to the adjacent populations with hooked spines than to those in Colorado with straight spines. Possibly they are not more important taxonomically than spineless phases of other plants scattered through spined taxa elsewhere in the Cactaceae. A peculiar phase from the Pariette Draw region of southeastern Duchesne County has a long juvenile stage, with the initial

central spines very short (to 2 mm long) and hooked or straight. It does not seem to warrant taxonomic recognition.

Var. *roseus* (Clover) L. Benson [*S. havasupaiensis* var. *roseus* Clover; *S. intermedius* Peebles, type from Pipe Springs, Arizona; *S. whipplei* var. *intermedius* (Peebles) L. Benson; *S. parviflorus* var. *intermedius* (Peebles) Woodruff & Benson; *S. parviflorus* Clover & Jotter, type from Forbidding Canyon; *S. contortus* Heil, type from eastern Wayne County; *S. terrae-canyonae* Heil, type from Trachyte Wash]. Some tiny juvenile plants have pubescent spines, but the juvenile stage is apparently arrested in most portions of this variety. Salt and mixed desert shrub, pinyon-juniper, sagebrush, and ponderosa pine communities at 1125 to 2440 m in Carbon, Duchesne, Emery, Garfield, Grand, San Juan, Sevier, Uintah, and Wayne counties; Colorado, New Mexico, Arizona, and Nevada; 102 (xiv). This variety is almost as variable as the species itself. It has been treated previously at specific rank (as three separate species) and as consisting of two varieties. With the degree of variability exhibited, it is not surprising that so many divergent views should have developed; it is surprising that even more segregation was not attempted. *S. contortus* is a slender-spined phase in which the spines are contorted, a condition that seems

to be unworthy of consideration from a taxonomic standpoint. *S. terrae-canyonae* appears to be more substantially based, with its long slender spines and yellow flowers. There is little correlation, however, between flower color and spine length. Long-spined phases are more common in the southeastern portion of Utah, but the flowers of the long-spined phases are mainly pink to violet. The var. *intermedius* is more difficult to discount. In the extreme situations that variety has the uppermost central spine flattened and ribbonlike, commonly 1–3.5 mm wide at the base, with var. *roseus* (or *S. parviflorus* per se) having the uppermost spine merely flattened and mainly 0.7–1 mm wide. There are as many intermediates as there are extremes, and, until other diagnostic criteria are identified, it seems best to include all of the tremendous range of variation within an expanded var. *roseus* of *S. whipplei*.

Sclerocactus wrightiae L. Benson. Plants depressed-hemispheric to obovoid or short-cylindric, mainly 6–12 cm long and 4–8 cm

thick; ribs mostly 8–13; tubercles more or less developed; areoles circular to elliptic; juvenile spines glabrous; central spines 1–4, the lower one often hooked on at least the upper tubercles, mostly 10–20 mm long, the uppermost 1–2.5 cm long, flattened, 0.8–1.5 mm wide; radial spines 8–11, spreading; flowers 2–3.5 cm long; sepaloids green or variously tinged with red or brown; petaloids yellowish to white or pink; fruit ellipsoid, 9–12 mm long; seeds black, tuberculate, 3–3.5 mm long. Salt desert shrub and shrubgrass to juniper communities at 1460 to 1865 m on Mancos Shale (Bluegate, Tununk, Emery, and Ferron members), Dakota, Morrison, Summerville, and Entrada formations in Emery and Wayne counties; endemic; 14 (iii). The small flowers and short spines are evidently diagnostic. Occasional intermediates with *S. whipplei* var. *roseus* occur in Emery County near the Sevier County line—at edaphic ecotones marking the boundary between shale and sandstone members of the Mancos Shale Formation.